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Butterflies of fragmented wet grassland in Western European lowland forests: Effects of vegetation, connectivity and plot size

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ABSTRACT

Habitat fragmentation, as a result of habitat loss and degradation, is widely considered to be a major threat to biodiversity. Our study focused on the distribution, diversity and abundance of butterflies on 22 isolated plots, mainly consisting of wet grassland. The plots were surrounded by deciduous mixed forests and located in an agglomeration area close to Lake Zurich, Switzerland. In addition to vegetation parameters, we assessed structural connectivity, adapted to least cost distances, using digital surface and terrain models. The resulting mixed-effects models revealed on plot level that (1) Molinia meadows had a significantly positive effect on rarefied Simpson butterfly diversity, (2) structural connectivity had a highly significant negative impact on rarefied Simpson butterfly diversity, whereas (3) plot size showed a significant positive impact, and (4) higher butterfly abundance was strongly related to blossom density. Across plot level, Molinia meadows had a higher rarefied butterfly species richness and rarefied Simpson butterfly diversity than any of the other habitat types evaluated. Among the endangered target species, the preferences of the Alcon Blue *Phengaris alcon alcon* were consistent with (1) to (3), while those of the Marsh Fritillary's *E. aurinia aurinia* were not. (2) is discussed with regards to the predominant influence of habitat type, vegetation and plot size, relativizing the effect of structural connectivity on butterfly communities in presumably resilient metapopulations. Ongoing targeted maintenance measures in the study area provide a promising basis for the sustainable conservation of local butterfly communities in isolated wet grassland plots.

1. Introduction

The extent to which a landscape is fragmented and species habitats are isolated has a major impact on wildlife (Dover and Settele, 2009). If the remaining fragments are too far apart, species movement and dispersal throughout resource patches are affected, the recolonization of extinct patches is impeded, and the gene-flow is likely to be compromised, resulting in lower species diversity over time (Brückmann et al., 2010; Haddad et al., 2003). Habitat fragmentation, as a result of increasing habitat loss and degradation (Pereira et al., 2010), is widely considered to be one of the major threats for biodiversity on global, regional and local scales (Debinski et al., 2001; Hanski, 2005; Krauss et al., 2010). As the remaining fragmented grasslands are often small, the question arises if and how their species diversity and abundance are affected by structural connectivity, patch size, habitat quality, and the distribution of other grasslands around a specific core patch. Additionally, the permeability of the matrix between patches must also be considered, since matrix composition is known to influence inter-patch movements (Prevedello and Vieira, 2010; Ricketts, 2001). An inhospitable forest matrix can induce strong selection, as illustrated by the dispersal of the two stenotopic wetland butterfly species *Phengaris teleius* and *Phengaris nausithous* (Nowicki et al., 2014), which finally leads to reduced emigration rates. Poniatowski, Stuhldreher, Löffler and Fartmann (2018) and Münsch et al. (2019) conclude that maintaining high quality patches should be the primary focus for the conservation of specialist insects in fragmented landscapes, putting the importance of connectivity into perspective.

Between 1900 and 2010, around 80% of all wetlands in Switzerland, especially on the Swiss Plateau, disappeared (Lachat et al., 2010). Even though moors of particular beauty and national importance have been subject to strict protection in Switzerland since 1987, their quality has deteriorated. The fens and bogs have become drier, richer in nutrients, and in almost one third of the total area more woody plants have emerged (Klaus, 2007). Around 37% of all priority plant and animal

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species, i.e. endangered species or species for which Switzerland holds a special international responsibility, depend on moors and riparian zones (Bundesamt für Umwelt, 2019).

On a regional scale, the proportion of moorland areas in the Canton of Zurich decreased from 8.3% to 0.7% between 1850 and 2000. The number of moorland patches also went down from 4341 to 708, and the average patch size fell from 3.2 to 1.7 ha (Gimmi et al., 2011). Since moors surrounded by forest, which are the focus of this study, are often somewhat remote, many wetlands in forest clearings have been spared from agricultural intensification. For decades, they have been mown once a year in autumn without being fertilized or grazed. As a result, and despite their proximity to the densely populated Greater Zurich Area, many wet grasslands in forest clearings still represent intact habitats for specialist insects such as for the two endangered stenotopic target butterfly species Alcon Blue *Phengaris alcon alcon* (Denis & Schiffermüller, 1775) and Marsh Fritillary *Euphydryas aurinia aurinia* (Rottemburg, 1775) (Bolt et al., 2010; Sohni, 2016).

The vast majority of the butterflies in Switzerland are found on extensively used semi-natural meadows and pastures and semi-open habitats like sparse forests, including nearby ecotones such as grassy linear elements, hedges and forest edges. There are only a few butterfly species which develop exclusively or predominantly on wetlands. Most of them are specialized and sedentary, which is why they are very sensitive to interventions in their habitat (Wermeille et al., 2014; Van Swaay et al., 2006). Larval stages of monophagous and oligophagous butterflies exhibit a high host plant specificity (Klaiber et al., 2017), while adults often show a distinct preference for assorted nectar plants and generally prefer flower rich landscapes (Schweizerischer Bund für Naturschutz, 1987). Especially less mobile butterfly species depend on a network of suitable habitats to maintain resilient metapopulations (Thomas, 1995). Due to these complex requirements, butterflies respond rapidly to environmental changes, being representative for wider trends in insect abundance (Thomas, 2005). They are perceived as an important model group in ecology and conservation (Krämer et al., 2012). Furthermore, butterflies are one of the most popular insect groups and their flagship quality makes them excellent promoters of nature conservation projects (Schlegel et al., 2015).

Our study aims to investigate the butterfly species distribution, diversity and abundance on isolated plots, mainly consisting of wetlands surrounded by deciduous mixed forests. To the best of our knowledge, this specific scenario has not been investigated yet in major conservation studies. We considered both small-scale (plot level: alpha diversity) and large-scale effects (subarea level: gamma diversity). Explicitly, we addressed the following research questions:

(1) What are the effects of habitat type (plant societies), blossom density, and average vegetation height on butterfly species distribution, diversity and abundance on isolated grassland plots within forests?
(2) How do connectivity and plot size interact with butterfly species distribution, diversity and abundance, taking into account the inhibiting effect of the forest matrix between the plots?
(3) How do vegetation parameters, connectivity and plot size affect the preservation of two endangered stenotopic wetland butterfly target species, the Alcon Blue *Phengaris alcon alcon* and the Marsh Fritillary *Euphydryas aurinia aurinia*?

2. Methods

2.1. Study area and survey plot characteristics

We investigated 22 grassland plots, surrounded by deciduous mixed forest, in three subareas close to Lake Zurich in Switzerland. The subareas "Pfannenstiel" and "Rueti" (12 plots and 4 plots respectively) are situated north of the lake, and the subarea "Sihlwald" (6 plots) is located south of the lake. The altitudes range from 484 m a.s.l. to 820 m a.s.l. The plot sizes are between 0.14 and 4.79 ha and the transect length per plot was between 78 m and 1205 m (Appendix A, Table A1). 12 plots are part of the national moor inventory (Schweizer Bundesrat, 2017).

2.2. Characteristics of each survey plot

- More than 30% or at least 500 m^2 consist of typical moorland vegetation according to the plant society classification by Delarze et al. (2015), which are either calcareous small sedge fens (Caricion davallianae), tall sedge fens (Magnocaricion), Molinia meadows (Molinion) or meadowsweet meadows (Filipendulion). There is only one cut per year, mostly not before 1 September (a few vigorous subareas are already cut from 1 August, and a few nutrient-poor subareas not before 15 September).
- *Phragmites australis* (Cav.) Trin. does not exceed 10% of the plot size.
- Less than 30% of the plot size consists of dryer and extensively managed semi-natural grassland, with one or two (occasionally three) cuts per year, mostly not before 1 July.
- No fertilizers or pesticides are allowed (single plant application on dryer semi-natural grassland theoretically allowed).
- The adjacent mixed deciduous forest is at least 20 m deep and 10 m high.

2.3. Butterfly sampling and vegetation survey

On each survey plot, all butterfly species (Lepidoptera: Rhopalocera, including Hesperiidae) and burnet moths (Lepidoptera: Heterocera, Zygaenidae), hereafter referred to as "butterflies", were recorded along wavy line transects, slightly adapted to the transect count method developed by Pollard and Yates (1993). All individuals seen within 2.5 m on each side and 5 m in front of the recorder were counted at a slow walking pace five times per year between 27 May and August 22, 2016 (subarea "Sihlwald") and between 24 May and August 17, 2018 (subareas "Pfannenstiel" and "Rueti"). The surveys were only carried out between 10:00 and 17:00 CEST under mostly sunny weather conditions with cloud cover <20%, at wind strengths <3 on the Beaufort scale, and temperatures >17 °C. The sequence in which the plots were surveyed was alternated to avoid systematic daytime effects. The butterflies were visually identified with close-focus binoculars or caught with a sweep net, identified and then released. The nomenclature follows the Swiss Center of the Cartography of Fauna "info fauna – CSCF" (2019). The two species *Phengaris alcon* and *Euphydryas aurinia* are divided into two distinct subspecies, which have different distributions and Red List statuses in Switzerland. Therefore, we assigned subspecies nomenclature to *Phengaris alcon alcon* and *Euphydryas aurinia aurinia*.

Prior to the vegetation season, the butterfly transect on each plot was divided into subtransects which represented visually homogenous units of the plant societies mentioned above. For this purpose, we used recent aerial photographs from 2014 to 2015 (Kanton Zürich, 2019). The lengths of the subtransects were adjusted, if necessary, during the first field survey. The area of each habitat type within each plot was standardized according to the proportion of the total butterfly transect length leading through the corresponding habitat type.

The butterflies were counted separately for each subtransect and the respective time was also recorded. In the transition zone between the subtransects no butterfly counts were performed over a length of 5–10 m in order to reduce edge effects.

The mean vegetation height and blossom density of each plot were measured during the second and fourth butterfly sampling period with a random selection of 1 sampling point per 1000 m^2. Blossom density was assessed at sampling points with a diameter of 1.5 m, based on a reference table developed by Gehlker (1977). Vegetation height was measured using a bamboo stick and a cardboard disc. First, the bamboo stick was placed on the sampling point. The cardboard disc was then connected to the bamboo stick through a hole in the middle. Finally, the disc was dropped onto the vegetation, which allowed the vegetation

height to be measured (Table 1).

2.4. Connectivity metrics

We applied Hanski's Incidence Function Model IFM (Hanski, 1994), which is considered to be the most appropriate approach for detecting connectivity effects on species (Brückmann et al., 2010; Winfree et al., 2005). For each of the 22 survey plots *i* we used the following equation:

$$S_i = \sum_{i \neq j} e^{-\alpha * d_{ij}} * A_j^b$$

S_i is the structural connectivity of the survey plot *i*, and d_{ij} is the distance between the survey plot *i* and any other wetland plot *j* within a radius of 10 km around the survey plot *i*. A_j is the area of a wetland plot *j*, $\propto$ is the reciprocal of the average migration distance of the species or a species group, and parameter *b* scales the effect of emigration to the surrounding area. $\propto$ was set to 1, corresponding to an average species migration of 1 km per year, a value which is commonly used in ecological studies (Prugh, 2009), for example by Hanski et al. (1996) for the habitat specialist butterfly species *Melitaea cinxia*. We further tested values of $\propto = 0.2$ and $\propto = 0.5$, which resulted in highly correlated S_i - values (pairwise Pearson correlation, all $R > 0.64$, all $p < 0.001$). The parameter *b* scales the size of the surrounding plots and was set to 0.5, ensuring that the ratio of patch edge and patch area decreases as the patch sizes increases (Münsch et al., 2019). Values between 0.1 and 0.5 are typical for butterflies (Moilanen and Nieminen, 2002). We used patch center-to-center distances for all distance measures in this study.

Since we assume that the forest between the plots, which represents the matrix, also has an influence on functional connectivity (Ricketts, 2001), we included least resistance distances ("least cost paths") instead of Euclidean distances. In least cost models, different resistance weights, which quantify how permeable an element is for a particular species group, are given to particular landscape features. In this way, the most probable migration or dispersal route can be identified (Holderegger and Wagner, 2008). We applied Hanski's IFM connectivity index, as mentioned above, to the adapted distance values.

The permeability of the forest matrix between the plots was calculated according to the average vegetation height (difference between the Digital Surface Model DSM and the Digital Terrain Model DTM), according to Ewald et al. (2014). Within each 5 × 5 m grid cell, the proportion of 0.5 × 0.5 m grid sub-cells with an average vegetation height >2 m was calculated. Based on this, a resistance matrix grid was established with a basic resistance of 0.5 and a maximum resistance of 1.5 for 100% vegetation height >2 m. For geodata processing we used the R-packages "raster" (Hijmans and Van Etten, 2016), "rgdal" (Bivand et al., 2018) and "sp" (Pebesma et al., 2016). The costDistance command in the "gdistance"-package (Van Etten and van Etten, 2011), based on Dijkstra (1959), was then applied to calculate the distances with the least resistance between the centroids of our plots (gCentroid command of the "rgeos"-package by Bivand (2018)). To determine the size and the spatial arrangement of the wet grassland plots we used vector data sets for wetland habitats derived from the Swiss Ecological Network REN for wetland habitats (Bundesamt für Umwelt, 2018). DSM and DTM data were provided by the Canton of Zurich (Kanton Zürich, 2018).

2.5. Data analysis and statistics

The butterfly sampling effort varied due to the different survey plot areas and transect lengths. Since plots with higher species abundances are likely to have higher numbers of species, the species diversity is not representative of true differences between the plots (Gotelli and Colwell, 2001). To avoid this bias, we applied individual-based rarefactions which allowed us to calculate expected species richness and species diversity for samples with varying species abundances. For plot-level comparisons (alpha diversity), we applied the results of a rarefaction based on 100 butterfly individuals, which is approximately twice the number of individuals found on the plot with the lowest abundance. To compare habitat types across all 22 plots (gamma diversity), we summarized the habitat-specific numbers for individuals of each butterfly species. Subsequently, we performed a rarefaction on the basis of 300 butterfly individuals, which is approximately twice the sum of individuals found on all tall sedge fens, the habitat type with the lowest total butterfly abundance. The 95% confidence intervals were determined by means of bootstrapping. Data analysis was carried out using "iNEXT" R-package (Hsieh et al., 2016).

In addition to the rarefied species richness, we also used rarefied Simpson diversity (the reciprocal of the Simpson index) as a further measure of species diversity (hereafter referred to as Simpson diversity). The Simpson index measures the probability that two randomly selected individuals from a sample will be the same and it delivers meaningful results even with small sample sizes. Lower Simpson diversity is equivalent with reduced evenness in species assemblages (Magurran, 2004).

The butterfly species abundance data from all five surveys were pooled for each plot and for each habitat type within a specific plot, with subsequent standardization to 100 m habitat transect length.

Table 1
Overview of the predictors applied in this study.

Predictor		Type	Details
Habitat types of survey plots			
Wetland	Meadowsweet meadow[a]	metric	m^2, standardized according to proportion of total butterfly transect length leading through the corresponding habitat type
	Low sedge fen[a]	metric	
	Tall sedge fen[a]	metric	
	Molinia meadow[a]	metric	
	Semi-natural grassland[b]	metric	
Landscape characteristics			
	Study area (random factor)	nominal	Subareas "Pfannenstiel", "Rueti", "Sihlwald"
	Connectivity	metric	Hanski's Incidence Function Model IFM (Hanski 1994) with least cost paths. Based on local digital elevation and digital terrain models (areas of grid cells and grid sub-cells see text)
	Survey plot size	metric	m^2, possible wood enclosure excluded, total 22 plots
Vegetation parameters			
	Vegetation height	metric	Average height in cm at sampling points with 1.5 m diameter (ca. 1 sampling point per 1000 m^2)
	Blossom density	metric	% cover at sampling points with 1.5 m diameter (ca. 1 sampling point per 1000 m^2)

[a] Wetland vegetation with 1 cut per year, mostly after 1 September (few vigorous subplots already from 1 August, few nutrient-poor subareas not before 15 September). No use of fertilizers or pesticides.

[b] Extensively managed meadow with 1 or 2 (occasionally 3) cuts; first cut mostly not before 1 July (few subareas with fewer restrictions). No use of fertilizers or pesticides, except single plant application.

Due to the left-skewed distribution of the rarefied species diversity, the values were log ((max +1)- x)-transformed ("max" is the value of the plot with the highest rarefied species diversity) for all of the models in order to approximate normal distribution (Shapiro-Wilk normality test $p = 0.23$). Species abundance data per 100 m transect length were log-transformed (Shapiro-Wilk normality test $p = 0.53$) and Simpson diversity values were not transformed (Shapiro-Wilk normality test $p = 0.60$).

To evaluate the relative importance of plot size, connectivity, habitat type and vegetation parameters for butterfly species diversity and abundance, we first built a linear mixed-effects model with z-scored predictor variables, and with subarea as random factor. The resulting full model exhibited high variance inflation factors (*VIF*) > 10 for most of the predictors, indicating high collinearity. Explanatory variables with *VIF* > 10 should always be examined, and, if possible, avoided (Borcard et al., 2018). Therefore, we ran three independent linear mixed-effect-models using the lmer command (maximum likelihood fit) of the "lme4" R-package (Bates et al., 2014). We fitted predictors representing (1) habitat type, (2) connectivity/plot size, and (3) vegetation parameters (blossom density, vegetation height), with subarea included as random factor. All the predictors from these separate models delivered *VIF* < 3. Subsets of predictor variables for each of the three models were then ranked separately based on the Akaike Information Criterion (*AIC*), corrected for small sample sizes (*AICc*), using the dredge command from the "MuMIn" R-package (Barton, 2019). The model estimates and p-values, which were based on conditional averages, were determined using the model averaging function and included all candidate models with Δ *AICc* < 4 (Burnham and Anderson, 2002). Models with Δ *AIC* < 4 are considered to be equivalent (Bolker, 2008). The relative contribution of each explanatory variable was expressed by its importance value, which is equal to the sum of weights/probabilities for all candidate models with Δ *AICc* < 4. Since *AIC* -values can be difficult to visualize, we applied single predictor regression plots to depict the interactions. If necessary, quadratic terms were included to optimize the model fit. To evaluate model accuracy, we used adjusted R^2-values as goodness-of-fit measures (Welham et al., 2014).

3. Results

3.1. Overview of butterfly species and abundance

We observed 40 butterfly species and 5497 individuals across all 22 survey plots (Appendix B, Table B1) with a mean of 18.4 species per plot (±5.7 S.D.) and 250 individuals per plot (±248 S.D.). According to the Swiss Red List for butterflies, *Euphydryas aurinia aurinia* (Rottemburg, 1775) and *Phengaris alcon alcon* (Denis & Schiffermüller, 1775) are considered to be endangered (EN), and *Brenthis ino* (Rottemburg, 1775), *Cupido argiades* (Pallas, 1771) and *Melitaea diamina* (Lang, 1789) to be near threatened (NT) (Wermeille et al., 2014). *C. argiades* is a thermophilic species, which has rapidly expanded its distribution area in recent years, probably as a result of climate change (Vittoz et al., 2013). The other Red List species mentioned are wetland habitat specialists (Klaiber et al., 2017).

Table 2
Observed butterfly species richness and rarefied species richness/Simpson diversity of the habitat types investigated. N = number of patches of the respective habitat type, pooled over all 22 survey plots. i = interpolation, e = extrapolation. Rarefaction was performed with a 95% confidence interval, based on 300 butterfly individuals per habitat type. Habitat types for which the rarefaction did not reveal significant differences ($p > 0.05$) are marked with a common letter.

Habitat type	N	Total species (observed)	Species richness Rarefied for 300 individuals		Simpson diversity	
Molinia meadow	36	36	25.69±1.36 (i)	**A**	8.32±0.46 (i)	**A**
Low sedge fen	34	34	24.17±1.59 (i)	**AB**	5.98±0.39 (i)	**B**
Semi-natural grassland	31	31	23.78±1.95 (i)	**AB**	6.61±0.63 (i)	**B**
Meadowsweet meadow	31	31	21.66±1.89 (i)	**B**	3.56±0.30 (i)	**C**
Tall sedge fen	14	14	14.87±3.36 (e)	**C**	5.65±0.99 (e)	**B**

3.2. Butterflies' responses to habitat types

When evaluating the effect of habitat types, a rarefaction revealed that the expected species richness on Molinia meadows was significantly higher than that on meadowsweet meadows and tall sedge fens (Table 2). In turn, tall sedge fens had a lower expected butterfly species richness than all other habitat types. In terms of diversity, Molinia meadows yielded significantly higher expected Simpson diversity values than all other habitat types, whereas meadowsweet meadows delivered the lowest diversity values.

3.3. Butterflies' responses to connectivity and plot size

Single predictor regressions revealed a marginally significant positive effect of the plot size on the rarefied Simpson diversity, but no obvious impact on either rarefied butterfly species richness or butterfly abundance (Fig. 1 a, b, c). Connectivity showed a distinctly negative impact on rarefied Simpson diversity, but no apparent effect on rarefied species richness or abundance (Fig. 1 d, e, f).

3.4. Butterflies' responses to vegetation parameters

Blossom density had a highly significant positive effect on butterfly abundance, but it was more or less indifferent with respect to rarefied species richness and rarefied Simpson diversity (Fig. 2 a, b, c). Vegetation height had a significant positive impact on abundance and a humped effect on rarefied Simpson diversity. Rarefied species richness was slightly inhibited by increasing vegetation height, without being statistically significant though (Fig. 2 d, e, f).

3.5. Predictive models of butterflies' combined responses to habitat type, connectivity/plot size and vegetation characteristics

We built three linear mixed-effects submodels, as described in the Methods section, each with low collinearities among the predictor variables (*VIF* < 3). We then assessed the impact of the predictor variables according to their averaged conditional estimates (Table 3). None of the predictor variables had a significant effect on the rarefied butterfly species richness. Rarefied Simpson diversity was significantly higher in Molinia meadows and it also increased with growing plot size, whilst higher connectivity between the plots led to a significant decline. Higher proportions of meadowsweet meadows resulted in lower rarefied Simpson diversity values. Blossom density significantly promoted butterfly abundance whereas plot size and connectivity did not appear to have any obvious impacts.

The abundance of the first target wetland butterfly species, the Marsh Fritillary *Euphydryas aurinia aurinia*, was not significantly affected by a specific habitat type, but the species seemed to favour Molinia meadows and to avoid meadowsweet meadows and tall sedge fens to some extent (Table 4a). While plot size and connectivity had no effect on the abundance, vegetation height had a marginally significant positive influence on the Marsh Fritillary. Blossom density, on the contrary, had a marginally significant negative impact. Areas with higher proportions of Molinia meadows had a highly significant positive influence on the abundance of the Alcon Blue *Phengaris alcon alcon*, our second target butterfly species (Table 4b). Plot size had a marginal positive effect on the abundance of this species as well. In turn, better connectivity between the plots resulted in a highly significant reduction

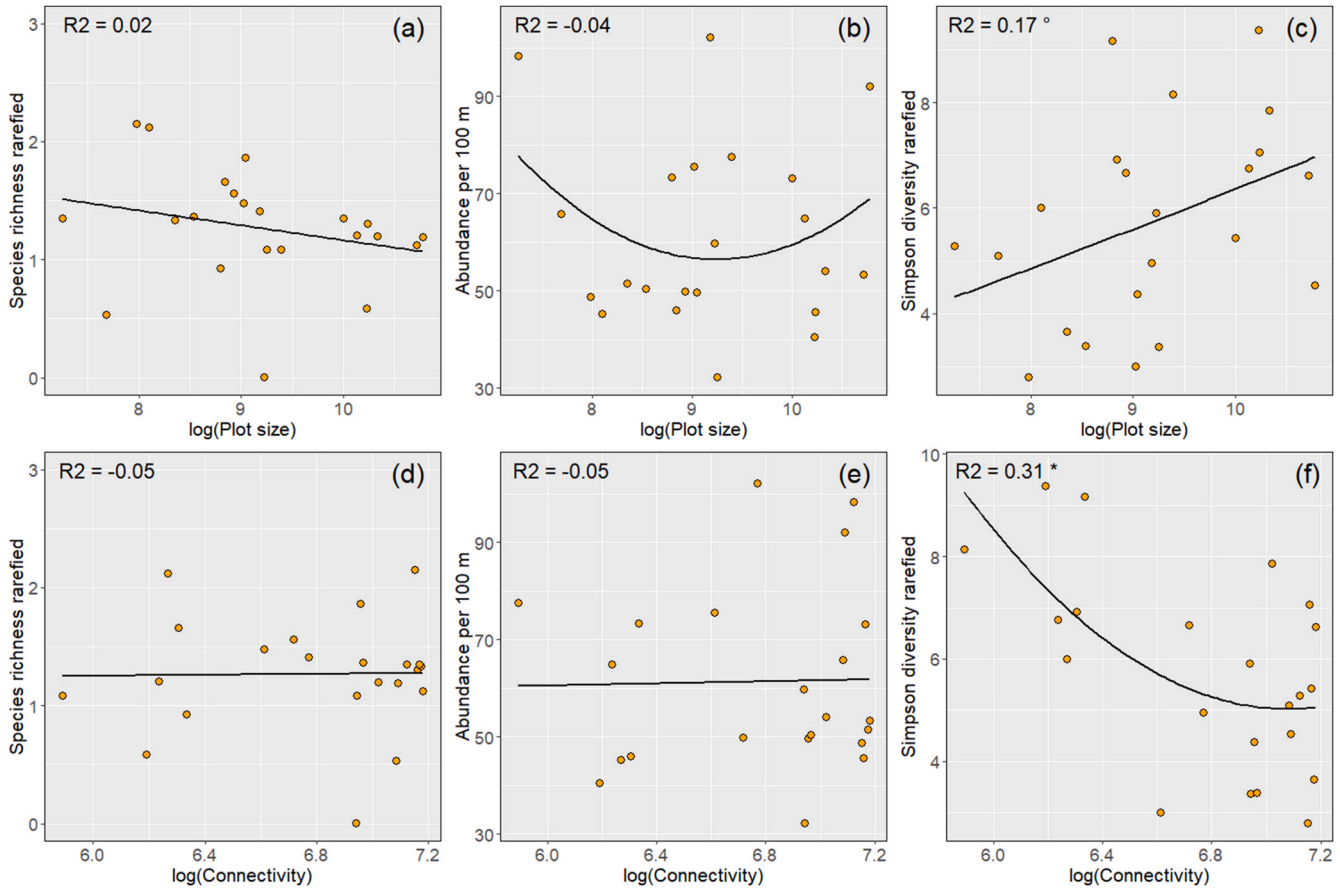

Fig. 1. Single predictor regressions for rarefied species richness (a, d), abundance (b, e) and rarefied Simpson diversity (c, f) of butterflies, with plot size and connectivity as separate predictor variables. R 2-values of (b) and (f) refer to regressions that included a quadratic term. *$p < 0.05$; ° $p < 0.10$.

of its abundance. Blossom density had a marginal negative influence on the abundance of the Alcon Blue.

4. Discussion

4.1. Butterflies' responses to habitat types with special regards to endangered local target species

On plot level, neither the predicted butterfly species richness, based on rarefactions, nor the total butterfly abundance per 100 m transect length were significantly dissimilar in small sedge fen, tall sedge fen, Molinia meadow, meadowsweet meadow and semi-natural grassland habitat types. On habitat type level, by summing up the habitat-related numbers of individuals of each butterfly species across all survey plots, Molinia meadows had the highest rarefied species richness and Simpson diversity scores. Tall sedge fens had significantly lower rarefied species richness scores than any of the other habitat types, while meadowsweet meadows had by far the lowest Simpson diversity scores. These outcomes illustrate the fundamental importance of the spatial perspective: For the butterfly community of a specific plot, in our case an isolated grassland plot surrounded by forest, the composition of the local habitat types is apparently not the key driver of species diversity and abundance. On the other side, from an overall perspective across all plots, habitat type is crucial for butterfly species richness and abundance. Various studies highlight evidence of the importance of the spatial scale for the assessment of biodiversity, ranging from the local scale (alpha diversity) to the regional or supraregional scales (gamma diversity). Yet, there is neither a consensus on the optimal scale to be used in butterfly studies and field works nor on the effect of different scales (Van Halder, 2017). Bergman et al. (2004) only found landscape effects on butterfly communities at the largest scale of 5000 m, while Krauss et al. (2003) and Marini et al. (2009) observed increases in species richness as landscape diversity increased at the smallest scale of 250 m and 95 m respectively.

On species level, the wetland target species Alcon Blue *Phengaris alcon alcon* showed a very close affinity for Molinia meadows. This butterfly is mainly known to occur on fens and Molinia meadows (Habel et al., 2007) with a sufficient number of host plants, preferably *Gentiana pneumonanthe* L. and, to some extent, *Gentiana asclepiadea* L. (Tartally et al., 2019). The subareas "Pfannenstiel" and "Sihlwald" are both known for their remarkable Alcon Blue metapopulations, both being hotspots for the nationwide conservation of this endangered species. The greater Pfannenstiel region was estimated to contain around 200 individuals of the Alcon Blue in 2009 (Bolt et al., 2010). In Northeast Belgium the occurrence of the Alcon Blue has most often been correlated with a dominance of *Molinia caerulea* combined with *G. pneumonanthe* (Maes et al., 2004). In central southern and eastern Europe, the myrmecophilic Alcon Blue's predominant host ant species is believed to be *Myrmica scabrinodis* Nylander, 1846 (Bräu et al., 2008; Mouquet et al., 2005). Bolt et al. (2010) confirmed this assumption for the Pfannenstiel region. The Marsh Fritillary *Euphydryas aurinia aurinia*, our second local endangered target species, only manifested weak affinities to any of the habitat types, including Molinia meadows. In southern Wales, however, the largest Marsh Fritillary populations can be found on grazed Molinia meadows (Lewis and Hurford, 1997), which is in line with observations of the Marsh Frittilary's subspecies *E. aurinia aurinia* on Molinia meadows in Italy (Casacci et al., 2015). In the UK, the Marsh Fritillary occurs in two distinct habitat types: on wet

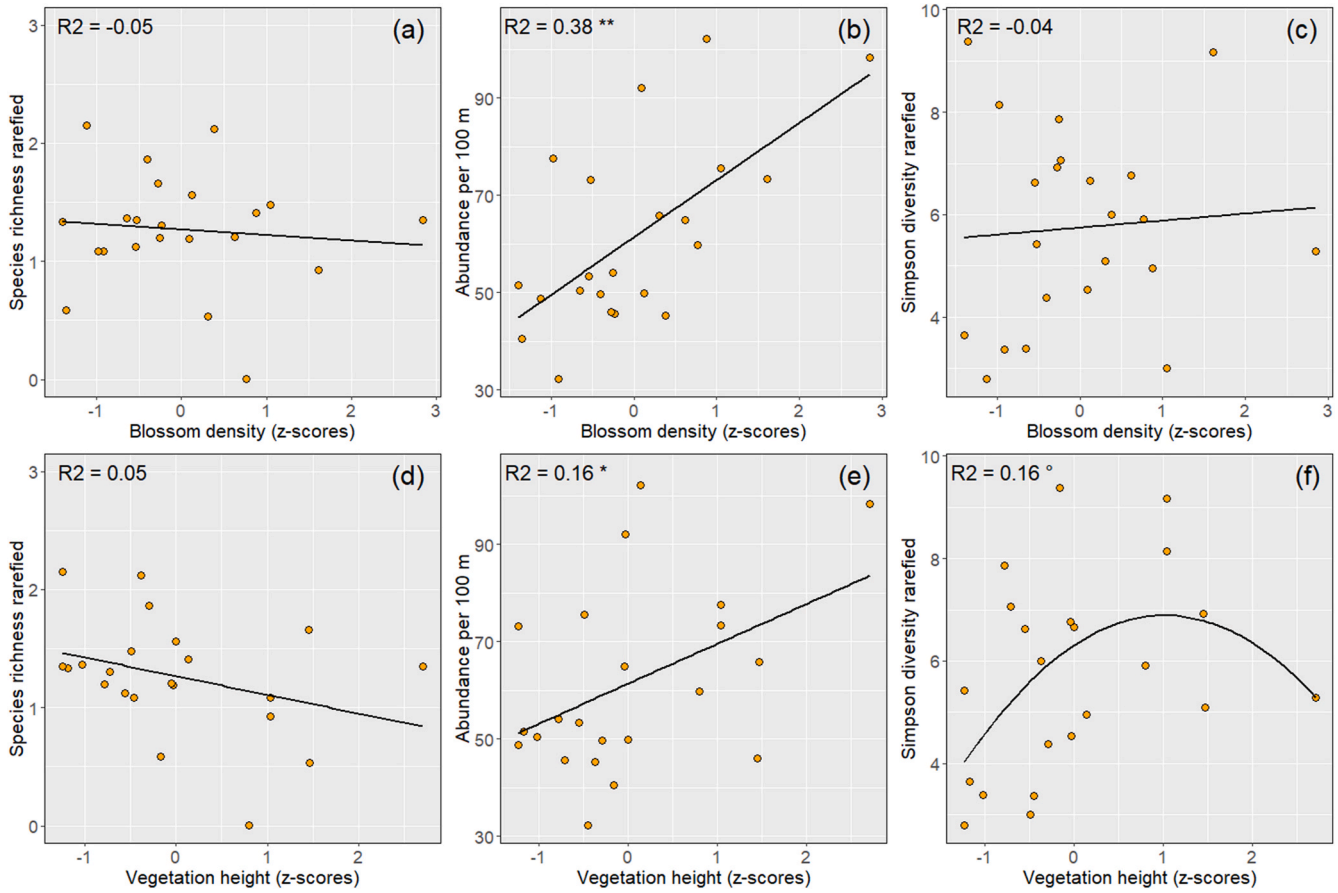

Fig. 2. Single predictor regressions for rarefied species richness (a, d), abundance (b, e) and rarefied Simpson diversity (c, f) of butterflies, with blossom density and vegetation height as separate predictor variables. R 2-value of (f) refers to a regression that included a quadratic term. **p < 0.01, *p < 0.05; ° p < 0.10.

and Molinia caerulea-dominated grasslands and on dry calcareous grasslands (Botham et al., 2011). The eggs are laid on two major host plants, *Succisa pratensis* and *Gentiana asclepiadea*. Optimal habitat conditions are assumed to exist on recently abandoned calcareous fen meadows and along the edges of currently used fen meadows (Anthes et al., 2003). Both host plants were frequent on all three of our subareas.

The predicted Simpson diversity per plot, based on rarefactions, revealed a strong pattern with Molinia meadows clearly yielding the highest values for butterfly diversity. This was because Molinia meadows not only had the highest number of expected butterfly species, but also exhibited more balanced relative species abundances than all other habitat types investigated. Alkaline Molinia meadows have been repeatedly considered to be one of the most species-rich of all grassland ecosystems in Central Europe in terms of fauna (especially insects), ranking immediately after dry and nutrient-poor semi-natural grasslands (Burkart et al., 2004). The high diversity found on Molinia meadows particularly seems to apply to grasshoppers (Schlumprecht and Waeber, 2003), butterflies (Dolek et al., 1999) and wild bee species (Moroń et al., 2008), findings that undermine the relevance of the preservation and appropriate maintenance of this wetland habitat type. In a nearby study area south of Lake Zurich, we investigated the effect of wetland habitat types on grasshopper species. The alkaline Molinion and meadowsweet meadows found there proved to have significantly higher Simpson diversity scores than low sedge fens, tall sedge fens or subareas with high densities of *Phragmites australis* (Schlegel and Schnetzler, 2018).

4.2. Butterflies' responses to connectivity

The connectivity between wetland plots only exerted a minimal effect on the predicted overall butterfly abundances and on the rarefied species richness, but higher connectivity had a distinctly negative impact on the rarefied Simpson diversity. The Alcon Blue *P. alcon alcon* was found in highly significant lower abundances in patches with higher connectivity, unlike the Marsh Fritillary *E. aurinia aurinia*, which remained indifferent to higher connectivity.

The average daily movement rates of European butterflies rarely exceed 200 m. Nevertheless, some species can easily migrate several kilometers (Bruppacher et al., 2016; Stevens et al., 2013). The missing impact of connectivity on the rarefied species richness in our study might be explained by the increasing evidence, that species formerly considered to be extremely sedentary are in fact able to move over distances similar to inter-patch distances found in real landscapes (Radchuk, WallisDeVries, & Schtickzelle, 2012).

The detrimental effect of higher connectivity on the rarefied Simpson diversity indicates a less balanced species composition with relatively few species occurring in high numbers, and with more species only occurring in low numbers. We checked this assumption for the four most common butterfly species in our study, namely (1) for the non-wetland generalist species *Aphantopus hyperantus* and *Maniola jurtina*, and (2) for the specialized wetland species *Melitaea diamina* and *Brenthis ino*. Separate linear mixed-effects models with subarea as random factor revealed a significant positive effect of connectivity on the generalist species *A. hyperantus* ($p = 0.05$), no significant effect of connectivity on *M. jurtina* ($p = 0.64$), and significant negative effects of connectivity on

Table 3
Linear mixed-effects models fitted to abundance, rarefied species richness and rarefied Simpson diversity, calculated separately for the submodels (1) habitat type, (2) connectivity/plot size and (3) vegetation parameters. Estimates and p-values of the predictor variables are based on conditional averages, the importance values refer to summarized weights of all candidate models with Δ *AICc* < 4, specified for each dependent variable separately. Rarefaction based on 100 individuals per plot, N = 22 survey plots, subareas defined as random factors. ***p < 0.001; **p < 0.01; *p < 0.05

Submodel	Dependent variable	Predictor variable	Importance value	Estimate (cond.)	p (cond.)
Habitat type	Abundance per 100 m (log)	Intercept		4.065	<0.001***
		Low sedge fen	0.11	0.059	0.456
		Meadowsweet meadow	0.11	0.055	0.427
		Molinia meadow	0.19	0.082	0.411
		Semi-natural grassland	0.08	−0.027	0.745
		Tall sedge fen	0.27	−0.113	0.207
	Species richness rarefied (log ((max +1)- x))	Intercept		1.268	<0.001***
		Low sedge fen	0.06	−0.008	0.946
		Meadowsweet meadow	0.25	−0.123	0.270
		Molinia meadow	0.29	−0.165	0.129
		Semi-natural grassland	0.07	−0.024	0.827
		Tall sedge fen	0.20	−0.139	0.205
	Simpson diversity rarefied	Intercept		5.770	<0.001***
		Low sedge fen	0.11	−0.251	0.451
		Meadowsweet meadow	0.21	−0.440	0.200
		Molinia meadow	**1.00**	**1.103**	**0.002****
		Semi-natural grassland	0.09	0.023	0.946
		Tall sedge fen	0.09	−0.075	0.870
Connectivity/Plot size	Abundance per 100 m (log)	Intercept		4.059	<0.001***
		Connectivity	0.16	−0.017	0.824
		Plot size	0.15	0.01	0.88
	Species richness rarefied (log ((max +1)- x))	Intercept		1.268	<0.001***
		Connectivity	0.14	0.005	0.965
		Plot size	0.24	−0.108	0.32
	Simpson diversity rarefied	Intercept		5.771	<0.001***
		Connectivity	**0.56**	**−1.126**	**0.001****
		Plot size	**0.71**	**0.748**	**0.029***
Vegetation parameters	Abundance per 100 m (log)	Intercept		4.059	<0.001***
		Blossom density	**1.00**	**0.177**	**0.001****
		Vegetation height	0.16	0.023	0.898
	Species richness rarefied (log ((max +1)- x))	Intercept		1.268	<0.001***
		Blossom density	0.20	0.016	0.909
		Vegetation height	0.44	−0.170	0.129
	Simpson diversity rarefied	Intercept		5.767	<0.001***
		Blossom density	0.15	0.103	0.763
		Vegetation height	0.23	0.345	0.323

the wetland specialists *B. ino* (p < 0.001) and *M. diamina* (p = 0.01). This leads to the conclusion, that *A. hyperantus*, by far the most common species in our data set, seems to be the main source of imbalance, leading to lower Simpson diversity values on survey plots with higher connectivity. Other frequent species, such as the wetland specialists *M. diamina* and *B. ino*, were not able to "correct" this overall picture of imbalance in well-connected plots.

In accordance with our outcomes, Hula et al. (2004) found no major effect on the Marsh Fritillary *E. aurinia aurinia* by overall landscape connectivity. On the other hand, we have no obvious explanation for the higher abundance of the Alcon Blue *P. alcon alcon* on isolated survey plots. At least it indicates that even on remote patches habitat conditions are likely to be intact for this highly specialized wetland species. Further research should reveal if host plant and host ant availability, or other still unknown parameters, differ between our survey plots, masking the effect of connectivity on the Alcon Blue (see Conclusions section). Various studies suggest that habitat quality overrules habitat connectivity for butterflies. Krauss et al. (2003) identified no significant impact on the butterfly community caused by habitat isolation, stating that habitat isolation appears to be less important, provided the butterflies can cope with the habitat mosaic. In another study, habitat quality explained patch colonization of stenotopic butterflies two to three times better than site isolation (Thomas et al., 2001). Increased connectivity has also been found to be ineffective at boosting the proportion of red-listed butterflies in landscapes with low matrix quality (Kormann et al., 2019). A mosaic of grasslands and woodlands has proven to be more effective than habitat connectivity for conserving butterflies in French farmland (Villemey et al., 2015). Other research projects, however, have delivered differing results, showing connectivity to have a positive influence when assessed together with habitat quality (Matter et al., 2009). Kormann et al. (2019) claim, that connectedness of habitat fragments can boost conservation benefits for butterflies in Germany, but only in landscapes with little cropland. Brückmann et al. (2010) also conclude, that connectivity is highly relevant for the conservation of butterfly species with specialized habitat requirements, but the decision as to which connectivity measure is most appropriate depends on patch configuration, landscape context and study design.

Fahrig (2017) states in a broad review that species' responses to habitat fragmentation is usually indifferent or even positive, in comparison to less fragmented landscapes with the same amount of the focus habitat. In other words, lower patch size and connectivity is not implicitly detrimental to species communities and ecosystem diversity, but it is always necessary to incorporate the permeability of the matrix with less suitable habitats between the patches in connectivity calculations (Debinski et al., 2001), especially with respect to less mobile species. If trapped in small and isolated habitat patches, such vulnerable species are prone to disadvantageous demographic effects and impeded gene flow, which could lead to local extinction.

4.3. Butterflies' responses to plot size

The unrarefied number of butterfly species increased significantly

Table 4
Linear mixed-effects models fitted to the abundance of the wetland target species **(a)** Marsh Fritillary *Euphydryas aurinia aurinia* and **(b)** Alcon Blue *Phengaris alcon alcon*, calculated separately for the submodels (1) habitat type, (2) connectivity/plot size and (3) vegetation parameters. Estimates and p-values of the predictor variables are based on conditional averages, the importance values refer to summarized weights of all candidate models with Δ *AICc* < 4, specified for each dependent variable separately. N = 22 survey plots, subareas defined as random factors.**p < 0.01; *p < 0.05; ° p < 0.10

(a) Marsh Fritillary *Euphydryas aurinia aurinia*

Submodel	Dependent variable	Predictor variable	Importance value	Estimate (cond.)	p (cond.)	
Habitat type	Abundance per 100 m (log)	Intercept		0.174	0.028	*
		Low sedge fen	0.06	0.001	0.987	
		Meadowsweet meadow	0.33	−0.123	0.126	
		Molinia meadow	0.25	0.144	0.208	
		Semi-natural grassland	0.06	0.006	0.946	
		Tall sedge fen	0.34	−0.145	0.194	
Connectivity/ Plot size	Abundance per 100 m (log)	Intercept		0.174	0.034	*
		Connectivity	0.16	−0.012	0.882	
		Plot size	0.16	0.013	0.874	
Vegetation parameters	Abundance per 100 m (log)	Intercept		0.170	0.032	*
		Blossom density	**0.50**	**−0.180**	**0.095**	°
		Vegetation height	**0.63**	**0.204**	**0.060**	°

(b) Alcon Blue *Phengaris alcon alcon*

Submodel	**Dependent variable**	**Predictor variable**	**Importance value**	**Estimate (cond.)**	**p (cond.)**	
Habitat type	Abundance per 100 m (log)	Intercept		0.483	0.0098	**
		Low sedge fen	0.10	−0.118	0.536	
		Meadowsweet meadow	0.08	0.013	0.950	
		Molinia meadow	**0.89**	**0.534**	**0.009**	**
		Semi-natural grassland	0.14	−0.177	0.351	
		Tall sedge fen	0.21	0.301	0.278	
Connectivity/ Plot size	Abundance per 100 m (log)	Intercept		0.483	0.007	**
		Connectivity	**0.92**	**−0.575**	**0.003**	**
		Plot size	**0.48**	**0.336**	**0.060**	°
Vegetation parameters	Abundance per 100 m (log)	Intercept		0.503	0.047	*
		Blossom density	**0.62**	**−0.536**	**0.064**	°
		Vegetation height	**0.50**	**0.504**	**0.086**	°

with plot size ($p < 0.001$, $R^2 = 0.69$, not shown above), which is in accordance with the findings of other authors who have investigated species-area effects (Connor and McCoy, 2001; He and Legendre, 2002), including butterflies (Peintinger et al., 2003; Steffan-Dewenter and Tscharntke, 2000). A German study revealed that population densities for specialist butterfly species increased as habitat area increased, but only had marginal impacts on generalists (Cozzi et al., 2008). After performing individual-based rarefactions on 100 butterfly individuals per plot, the effect of plot size on the species numbers in our study diminished and turned out to be marginally negative. The influence of plot size on the rarefied Simpson diversity, however, was still significantly positive, while butterfly abundance was mostly unrelated to plot size. In other words, the higher species numbers in larger plots are linked to the inherently higher absolute numbers of individuals (area--abundance relation). The species abundance ratios in our study showed more balanced structures in larger plots, thus resulting in higher rarefied Simpson diversity values. Fahrig (2020) made a comprehensive review of 75 studies across a wide variety of taxonomic groups in which the sampling effort was proportional to patch size. Over 90% of these studies provided evidence that small patches usually hold more species than larger patches of the same total area, which is consistent with our rarefied species richness outcomes. Mean patch size also correlated negatively to butterfly species richness in a multiple scale context-study by Kumar et al. (2009). The authors suggest that butterflies on smaller plots might benefit from (1) more pronounced edge effects, which could provide suitable microhabitats, (2) higher host plant densities, and (3) higher plant species dissimilarities, whereas high forest cover might hinder butterfly movement. Harrison and Bruna (1999) and Soga et al. (2013) point out that higher edge/area-ratios on small habitat islands are evident for the species composition. For the endangered open habitat specialist species Alcon Blue *Phengaris alcon alcon* (Klaiber et al., 2017), we found marginally significant positive area-abundance-ratios. The smallest patch on which the Alcon Blue occurred was approximately 8300 m^2. On all of the 8 smaller patches, ranging between 3300 m^2 and around 7600 m^2, the Alcon Blue was absent, while on 10 out of the 12 plots that ranged between 8300 m^2 and 47,900 m^2 the species was present, with the highest abundances found on plot sizes over 12,000 m^2. As mentioned above, the life cycle of the Alcon Blue is strongly dependent on the presence of *Gentiana pneumonanthe*, which itself needs sunny habitats (Lauber et al., 2012). In turn, Maes et al. (2004) point out that in the Benelux countries the Alcon Blue is able to survive in small habitat units < 1 ha, even with low host plant densities, provided suitable host ants are present. However, we have to keep in mind that extinction risks are higher for small patches if reproduction does not keep pace with emigration, and if compensation through immigration is insufficient (Dover and Settele, 2009; Kindvall and Petersson, 2000).

Succisa pratensis, the preferred host plant of the Marsh Fritillary *Euphydryas aurinia aurinia*, is thought to be slightly more shade-tolerant than *G. pneumonanthe* (Lauber et al., 2012). Therefore, the effect of plot size on the presence of the Marsh Fritillary might, with respect to its host plant, be less pronounced. In our survey, a single individual was even found in the second smallest wetland plot, which measured approximately 2200 m^2. In a UK-study, almost half of the Marsh Fritillary colonies were associated with small patches <2 ha and only one sixth occupied patches larger than 10 ha (Warren, 1994). The decline of the Marsh Fritillary in the Czech Republic, in contrast, was clearly associated with small habitat size (Hula et al., 2004).

When assessing the presence of Red List butterflies (*Brenthis ino*, *Cupido argiades*, *E. aurinia aurinia*, *Melitaea diamina*, *P. alcon alcon*), we found that all of them were bound to wetlands, except for *C. argiades* (Klaiber et al., 2017), and that plot size had no significant influence on their overall abundance (separate linear mixed-effects model, $p = 0.44$, not shown above). These outcomes are mainly due to the high frequencies of *B. ino* and *M. diamina*, which together accounted for nearly

93% of all Red List individuals. The occurrence of *B. ino* turned out to be positively related to increasing habitat area at higher elevated sites in the Swiss Alps (Cozzi et al., 2008). Botham et al. (2015) claimed that lepidoptera communities were expected to show a positive response to habitat area, particularly in terms of abundance, because of their narrow niche requirements. As shown above, this kind of abundance pattern could not be detected in our study area, neither for butterflies as a whole, nor for the Red List habitat specialists in particular.

4.4. Butterflies' responses to vegetation parameters

Blossom density had a significant positive effect on the predicted butterfly abundance, but almost no influence on the butterflies' rarefied species richness and rarefied Simpson diversity. The availability of feeding resources has been regarded as one of the main elements that determine habitat quality for butterflies (Dennis and Sparks, 2006). In addition, the abundance and distribution of host plants is believed to control the development of butterfly caterpillars (Dennis, 2012; Kalarus and Nowicki, 2015). Blossom density positively influenced species richness and the abundance of butterflies on grassland sites in southern Germany (Habel et al., 2019), whereas Steffan-Dewenter and Tscharntke (2000) did not find comparable effects at another study site with similar habitat types. The marginally significant negative effect of blossom density on the Alcon Blue and the Marsh Fritillary in our study might reflect either a sufficient supply of nectar resources on the isolated wetland plots or, if further dispersal were to take place, the effect of nearby flower-rich farmland. Flower-rich meadows have recently been established to promote nectar-dependent insects, mainly in the "Pfannenstiel" subarea (Sohni, 2016).

5. Conclusions and conservation implications

Since the structural connectivity of the wetland plots and the potentially impeding effects of the forest matrix had no major impact on the expected overall butterfly species richness in our study area, we (1) suggest that the spatial configuration of the wetland habitat network might be appropriate for the short-term preservation of the local butterfly communities on a local scale, assuming mostly intact metapopulation structures. However, we have no insight yet into individual-based inter-patch movements and to what extent forested areas are traversed or overflown by specific butterfly species. The missing effect of higher connectivity could (2), additionally or alternatively, indicate that the availability of resources on the various wetland plots is sufficient to host more or less sedentary butterfly populations with perhaps only sporadic species' dispersal between the wetland patches. This is not necessarily contradictory to the minimal area requirements of butterflies, which range, among the species present, from below 1 ha for *Brenthis ino* or *Melanargia galathea* to 50 ha or more for *Limenitis camilla* or *Papilio machaon* (Maes et al., 2004; PAN Partnerschaft, 2017). Investigations of different insect groups have proved that species dispersal is rarely completely inhibited by impassable distribution barriers, even if the habitats give the impression of being isolated. The genetic flow can be maintained even in highly fragmented agricultural landscapes (Keller, 2012). In a landscape that we perceive as highly fragmented, the exchange between populations of mainly smaller animal species does not seem to be completely restricted (Bolliger and Gugerli, 2017).

The lower rarefied Simpson diversity values on better connected wetland patches indicate, however, species-specific differences in dispersal intensity and settlement patterns. As illustrated by the endangered Alcon Blue, one of our main representatives of stenotopic wetland butterfly species, wetland plot size, the proportion of Molinia meadows and blossom density seem to be the main drivers of higher population densities. Further research should reveal whether host plant and host ant availability meet the requirements of the Alcon Blue on large isolated patches of Molinia meadows. Nevertheless, we should be aware that the current situation for the butterfly fauna does not represent the present quality of habitats and habitat management. For grassland butterfly species that require large habitat areas, extinction debts of half a century after habitat deterioration (Sang et al., 2010) prove that such a time delay could affect stenotopic wetland specialist species in our study area as well. The richness of grassland specialist butterflies was better explained by past than present landscape conditions in a study by Löffler et al. (2020). To counteract future biodiversity loss, the Canton of Zurich has implemented differentiated management strategies for wetlands with a focus on asynchronous management. This includes late autumn cuts in areas with late flowering plants, e.g. *Gentiana pneumonanthe* and *Succisa pratensis*, the main host plants for the Alcon Blue *Phengaris alcon alcon* and the Marsh Fritillary *Euphydryas aurinia aurinia*. Being aware that habitat quality is species-specific, targeted conservation efforts may prove to be detrimental to other species in the same community (Baguette et al., 2013). Therefore, wetland promotion measures should, whenever possible, focus on specialized and endangered or on locally typical target species with umbrella status. We consider both of our existing local focal species, the Alcon Blue and the Marsh Fritillary to be appropriate representatives for such future conservation efforts. For a better understanding of the context between the distribution patterns and their host plant availability (incl. host ant presence for the Alcon Blue) we propose follow-up studies on the current and on additional survey plots. A noteworthy approach is provided by Maes et al. (2004) and Ries and Debinski (2001), considering the high returning probabilities of sedentary butterfly individuals that approach the edge of their habitat. The higher the trees at the edge of the habitat, the more likely the species was to return. This knowledge could be used to maintain or create suitable forest edge structures, particularly when other suitable habitat is unavailable within colonization capacity (Maes et al., 2004). However, since undesired shading from tall marginal trees is likely to reduce the overall quality of the wet grasslands (Edelkraut and Güsewell, 2006; Komonen et al., 2013; Noreika et al., 2016), especially in smaller clearings, a situational assessment of the advantages and disadvantages is essential.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

Table A1

			Transect length (m)							
Plot	Subarea	Area (m2)	Total	Low sedge fen	Meadowsw. meadow	Molinia maedow	Semi-nat. grassland	Tall sedge fen	Latitude	Longitude
1	Pfannenstiel	47901	1205	424	126	130	525	0	N 47° 17.480	E 8° 40.035
2	Pfannenstiel	27877	770	436	0	0	334	0	N 47° 17.574	E 8° 39.806
3	Pfannenstiel	45143	1205	442	18	291	454	0	N 47° 17.720	E 8° 39.801
4	Pfannenstiel	4224	159	0	159	0	0	0	N 47° 17.610	E 8° 39.655
5	Pfannenstiel	1413	78	0	78	0	0	0	N 47° 17.678	E 8° 39.377
6	Pfannenstiel	2171	79	0	0	79	0	0	N 47° 17.747	E 8° 39.196
7	Pfannenstiel	2916	127	127	0	0	0	0	N 47° 17.810	E 8° 39.458
8	Pfannenstiel	22129	598	125	63	98	312	0	N 47° 17.880	E 8° 39.687
9	Pfannenstiel	30640	927	122	0	272	533	0	N 47° 17.947	E 8° 39.394
10	Pfannenstiel	7560	315	0	66	249	0	0	N 47° 18.430	E 8° 38.849
11	Pfannenstiel	9695	349	65	70	214	0	0	N 47° 18.580	E 8° 38.953
12	Pfannenstiel	8274	274	274	0	0	0	0	N 47° 18.881	E 8° 39.229
13	Rüti	8465	350	130	86	0	97	37	N 47° 15.350	E 8° 53.192
14	Rüti	10390	388	41	58	25	246	18	N 47° 15.384	E 8° 52.984
15	Rüti	10128	314	88	167	59	0	0	N 47° 15.525	E 8° 53.201
16	Rüti	5075	286	0	129	0	156	0	N 47° 15.592	E 8° 53.572
17	Sihlwald	6600	180	50	0	110	0	20	N 47° 16.582	E 8° 33.489
18	Sihlwald	6900	115	0	0	55	0	60	N 47° 16.531	E 8° 33.645
19	Sihlwald	27600	395	0	0	210	0	185	N 47° 16.209	E 8° 33.789
20	Sihlwald	25100	340	35	0	215	0	90	N 47° 16.013	E 8° 34.140
21	Sihlwald	3300	95	0	40	55	0	0	N 47° 15.899	E 8° 34.124
22	Sihlwald	12000	170	0	0	170	0	0	N 47° 15.587	E 8° 33.922
		Total	8719	2357	1061	2232	2658	410		

Appendix B

Table B1

Species	Plot																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Aglais io	1	0	1	0	4	1	0	0	4	0	2	1	0	0	1	0	0	0	0	0	0	0
Aglais urticae	4	1	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Anthocharis cardamines	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	0	0
Aphantopus hyperantus	417	86	124	40	29	20	35	137	95	46	119	110	70	65	60	66	22	7	21	58	13	28
Araschnia levana	7	1	2	1	2	1	0	8	1	4	0	2	2	6	3	3	12	3	3	5	1	4
Argynnis paphia	23	26	8	2	9	3	3	2	7	8	35	9	5	6	26	4	6	5	7	10	2	15
Boloria euphrosyne	0	1	0	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brenthis ino	56	13	27	4	2	2	2	22	33	18	19	12	28	3	13	1	22	11	21	26	4	25
Carterocephalus palaemon	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	2
Celastrina argiolus	0	0	2	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Coenonympha pamphilus	1	0	1	0	0	0	0	1	4	0	0	0	0	1	0	2	1	0	0	2	0	0
Colias alfacariensis/hyale	1	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Cupido argiades	1	0	0	0	0	0	0	2	1	0	3	1	0	0	0	0	0	0	0	0	0	0
Cyaniris semiargus	12	2	2	0	0	1	0	3	4	4	4	2	0	0	2	1	0	0	2	2	0	2
Erynnis tages	0	1	0	0	0	0	0	0	0	2	1	4	1	0	1	0	0	0	3	1	0	1
Euphydryas aurinia aurinia	1	2	6	0	0	1	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	3
Fabriciana adippe	4	1	0	0	0	0	0	0	3	0	3	1	0	0	5	0	0	0	0	0	0	0
Gonepteryx rhamni	2	2	4	0	10	2	0	1	0	0	2	1	1	0	6	2	6	5	9	8	4	6
Issoria lathonia	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptidea sinapis/juvernica	4	0	4	0	0	0	0	0	2	1	2	0	0	0	2	0	2	0	0	2	1	0
Limenitis camilla	0	0	0	1	0	1	1	0	1	1	0	0	1	1	2	3	0	0	0	0	0	3
Lycaena tityrus	2	0	3	0	0	0	0	2	3	0	0	0	0	2	0	1	2	0	0	0	0	0
Lysandra bellargus	21	15	9	0	0	0	0	4	3	0	0	0	0	0	0	0	0	0	0	0	0	0
Maniola jurtina	253	54	72	12	5	4	0	64	72	14	10	3	20	12	32	40	11	6	17	40	7	25
Melanargia galathea	126	60	165	5	1	1	1	94	78	15	2	0	0	8	1	5	0	0	1	0	0	0
Melitaea diamina	32	34	54	6	3	7	10	14	51	23	88	41	21	7	15	5	19	23	30	26	3	35
Ochlodes sylvanus	36	15	14	3	7	8	7	29	21	5	20	7	16	2	5	1	11	5	15	19	8	28
Papilio machaon	10	0	0	0	1	0	0	2	0	0	0	0	1	0	0	0	1	1	3	0	0	1
Pararge aegeria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1

(*continued on next page*)

Table B1 (*continued*)

Species	Plot																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Phengaris alcon alcon	10	1	4	0	0	0	0	1	2	0	2	1	0	0	2	0	0	0	11	2	0	10
Pieris brassicae	12	7	8	1	2	0	1	4	5	9	6	3	1	0	2	0	0	0	0	0	0	0
Pieris napi	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	2	2	1	0	0
Pieris rapae	10	2	5	3	0	0	0	4	2	4	4	4	0	2	4	3	4	3	4	2	0	0
Polygonia c-album	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	2
Polyommatus icarus	37	16	45	1	1	0	2	20	40	3	29	2	4	5	3	5	5	0	5	9	0	0
Pyrgus malvae	1	0	2	0	0	0	0	0	0	0	0	0	1	2	0	1	4	0	0	2	0	0
Satyrium w-album	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Vanessa atalanta	3	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	1
Vanessa cardui	1	0	2	0	0	0	0	0	2	0	1	0	0	0	1	0	2	4	4	5	0	2
Zygaena filipendulae	20	9	75	0	0	0	0	18	64	0	3	0	0	0	0	0	0	0	0	0	0	0
Total individuals	1110	352	644	82	77	52	62	438	502	157	357	207	174	125	188	144	132	76	160	221	43	194
Abundance (per 100 m transect length)	92	45.7	53.4	51.5	98.2	65.8	48.7	73.2	54.1	49.8	102.2	75.6	49.7	32.2	59.8	50.4	73.3	46.0	40.5	65	45.2	77.6
Total species	31	22	27	14	14	13	9	25	26	15	22	19	16	17	22	17	17	13	18	19	9	19
Species richness (rarefied for 100 individuals)	15.5	15.1	15.7	15.0	15.0	17.1	10.2	14.9	15.5	14.0	14.7	14.4	12.4	15.8	17.8	14.9	16.3	13.5	17.0	15.5	10.4	15.8

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